

Hundred-year decline of North Atlantic predatory fishes

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Abstract

We estimate the biomass of high-trophic level fishes in the North Atlantic at a spatial scale of 0.5° latitude by 0.5° longitude based on 23 spatialized ecosystem models, each constructed to represent a given year or short period from 1880 to 1998. We extract over 7800 data points that describe the abundance of high-trophic level fishes as a function of year, primary production, depth, temperature, latitude, ice cover and catch composition. We then use a multiple linear regression to predict the spatial abundance for all North Atlantic spatial cells for 1900 and for each year from 1950 to 1999. The results indicate that the biomass of high-trophic level fishes has declined by two-thirds during the last 50-year period, and with a factor of nine over the century. Catches of high-trophic level fishes increased from 2.4 to 4.7 million tonnes annually in the late 1960s, and subsequently declined to below 2 million tonnes annually in the late 1990s. The fishing intensity for high-trophic level fishes tripled during the first half of the time period and remained high during the last half of the time period. Comparing the fishing intensity to similar measures from 35 assessments of high-trophic level fish populations from the North Atlantic, we conclude that the trends in the two data series are similar. Our results raise serious concern for the future of the North Atlantic as a diverse, healthy ecosystem; we may soon be left with only low-trophic level species in the sea.

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'You see something and then you try everything you can think of to make it go away; you turn it upside down and inside out, and push on it from every possible angle. If it's still there, maybe you've got something' (Cole 1998, p. 96)

Introduction

How is the world doing today? We often tend to stick to *Terra firma* when reflecting on this question, but the oceans have a role to play as well. We know that global climate is closely linked to the oceans' circulation patterns, and that the oceans serve as a major food source, two roles too important to jeopardize. In that connection, it has been comforting to hear, as we have for decades, that the food supply from the oceans keeps increasing, but that comfort is beginning to erode with reports that the global catches have been decreasing for the last decade (Watson and Pauly 2001). We hear of a fisheries crisis in the North Sea, in North-eastern Canada; actually we have heard of fisheries crises about everywhere regularly for the last couple of decades. What is happening to the fish in the ocean?

We have to be concerned for several reasons, with food supply being a major factor. But, our concern goes beyond this; we have seen drastic changes in ecosystem structure in a number of marine systems, a notable example being the Black Sea (Daskalov 2002), and there is fear that ecosystems may change to alternate stable states if severely disturbed. We have also seen repeatedly that once fish populations collapse, it may take decades for them to rebuild, perhaps because compensatory effects may lead to such changes in ecosystem states (Walters and Kitchell 2001).

To minimize the risk of adversely impacting the oceans, we should seek to maintain healthy ecosystems. Legislation to ensure this is by now incorporated in laws and policy directives of many countries (e.g. Canada's Ocean Act, USA's Magnuson-Stevens Act, and the EU Common Fishery Policy), as well as in the UN Convention on the Law of the Sea where nations have accepted a mutual obligation to take all appropriate actions to preserve the marine environment. An important part of this is to maintain sufficient stock sizes at all trophic levels as a safety margin, avoiding the process of fishing down the food web, where predatory species are gradually eliminated (Pauly *et al.* 1998), since the hope that we may be able to replace the predators in the sea is unfounded (Christensen 1996). Perhaps, we should

make comparisons to stock portfolio theory: a safe portfolio is diversified, hedging a bet on many different sectors. Our living marine resources should be managed in a similar way if we are to see but short-term gain and long-term loss; mining is not a viable option for managing living resources.

How much fish is there then in the sea? This is a crucial question for management of individual stocks in individual areas, and, in that context, a question for which we have, at hand, a suite of approaches for addressing it. Our interest in the present study is, however, wider: we are asking the question with regard to all species in a large area: how much fish is there in the North Atlantic?

Even before embarking on an attempt to quantify the total fish biomass, we know that any estimate will be very uncertain. However, just as is the case for stock assessments, the biomass of fish in itself is not of real importance; what is relevant is how the biomass of fish has changed over time. Recognizing this *a priori*, we refine the question: how has the biomass of fish in the North Atlantic changed over the last 100 years?

We focus our study on the last half of the 20th century, partly because we cannot expect to see any clear trends if the time period is too brief, and partly because the 50-year period will cover the period following the relative peace (for the fish) of the Second World War up through a period with strong industrialization and expansion of the North Atlantic fisheries, and onwards to the years of fisheries collapses that have characterized the end of the 20th century across the North Atlantic.

Estimating basin-level abundance of fish is a novel idea, as fisheries science has so far always worked on smaller scales (Pauly and Pitcher 2000) and we are not familiar with any previous attempts we could use for guidance. Fisheries science does not have much tradition of addressing questions at such level, at least not questions that go beyond the amount of catch that may be extracted from the oceans (Pauly 1996). In recent years, however, we have seen more interest in reconstructing prior states of ecosystems (an early example of this is given in Christensen and Pauly 1998), and find it important to look beyond our own time horizon when evaluating the state of the oceans (Pauly 1995).

In seeking to estimate the total fish abundance, we may take two different routes. One is a bottom-up approach where we would attempt to estimate the abundance of the individual species and sum these abundances up to the North Atlantic level. Such an

approach is, however, not likely to succeed; for one, we only have abundance estimates of a few populations of fish (Caddy *et al.* 1998), and the chance of actually going out and measuring how much fish there is in the sea is a formidable task beyond the capacity of any research group. Instead, we adopt a modelling approach where we use a number of spatial ecosystem models to quantify how much life there is in the area and at the point in time characterized by each model. We then use the physical and biological properties of the 0.5° latitude by 0.5° longitude grid cells in the area covered by the individual models in a multiple linear regression to search for patterns that may predict how abundance is distributed over space and time.

The objective to estimate the abundance of fishes in the North Atlantic calls for a level of aggregation, the species level being too detailed. One option is to summarize the abundance of fishes by trophic level. We know the average trophic level for each group from either diet composition studies (e.g. through FishBase) or ecosystem models (e.g. Ecopath), and the models tell us how individual groups are distributed between trophic levels. Hence, it becomes feasible to estimate the abundance of fish at, e.g. trophic level 4. However, apart from herrings, we do not have much knowledge about the fish abundances at the lower trophic levels, e.g. for the smaller forage fishes. This reflects the fact that forage fishes have been of little interest historically, and that the sampling methods in general use are unable to sample small fishes reliably.

Indications about historic abundances of, e.g. menhaden in Chesapeake Bay, points to the sea being full of forage fish, while some studies indicate that the abundance of forage fishes may have increased in recent time due to cascading effects caused by decreasing predator abundance as a result of human exploitation, e.g. for capelin in the Newfoundland area (Carscadden *et al.* 2001), and for small pelagics in the Black Sea (Daskalov 2002). However, the evidence for cascading in marine ecosystems is inconclusive (Pace *et al.* 1999; Pinnegar *et al.* 2000), and while the jury is out, we avoid the controversy here by not dealing with the lower trophic levels.

Thus, in this study, we focus on high-trophic level fishes, reflecting that these organisms serve as indicator species for the health status of marine ecosystems. The pattern emerging from studying human impact on a variety of systems shows repeatedly that the top predators are the first to go when fishing turns

intensive – even if pelagics are more known for exhibiting dramatic collapses (Pauly *et al.* 1998).

As tools of analysis for assessing the biomass of fish in the North Atlantic, we have constructed a series of ecosystem models of North Atlantic ecosystems as part of the 'Sea Around Us' project (SAUP), and use these together with published models from various areas in the North Atlantic to obtain a wide spatial and temporal coverage. The models have varying levels of spatial coverage and details. This paper provides an outline for how such a strategy has been implemented to address basin-level questions, and presents results from the data extraction that has been conducted based on the models.

Methodology

The methodology we have used to predict the biomass of fish in the North Atlantic relies on a combination of ecosystem modelling, information from hydrographic databases, statistical analysis and GIS modelling. A flowchart for this approach is presented in Fig. 1 to guide further reading.

Ecosystem models from the North Atlantic

The available information about biomasses at the ecosystem level is very incomplete, making it necessary to rely on modelling to obtain a coherent picture of the distribution and abundances of fish in the North Atlantic. We can base the modelling on the array of information that is available at the population level, mainly due to stock assessments made as part of the regulatory process. In addition, we have information from research surveys (which serve as a major information provider for the assessments), as well as from biological oceanographic studies. A major part of the biological and ecological information required for construction of the ecosystem models is available from the FishBase database, available online at <http://www.fishbase.org>. The aim of the modelling efforts is to combine such information to derive a realistic picture of biomasses and their interaction in a series of ecosystems throughout the North Atlantic.

In the present study, we rely on ecosystem models constructed using the widely distributed Ecopath with Ecosim (EwE) approach and software for which Christensen and Walters (2000) and Pauly *et al.* (2000) gave overviews of its capacity and limitations. Ecopath models are intended to summarize the abundances and interactions of all major functional

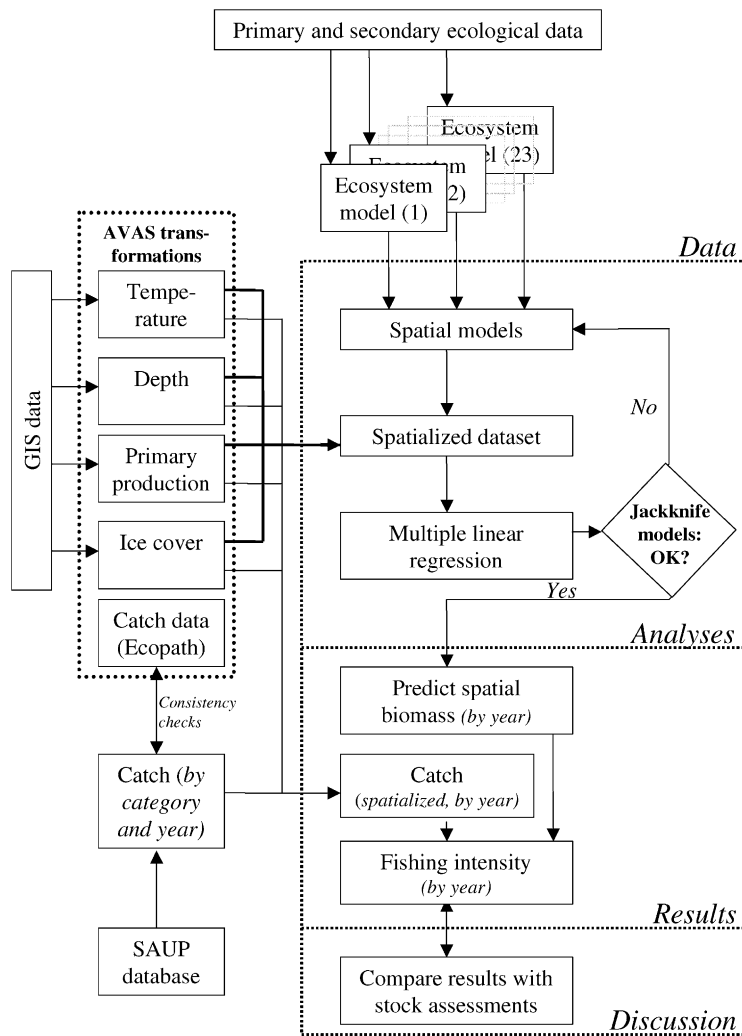


Figure 1 Schematic overview of the methodology used for predicting the biomass of high-trophic level fish in the North Atlantic.

groups in an ecosystem, along with detailed descriptions of how we exploit such ecosystems through fishing activities. A typical Ecopath model (such as the bulk of those on which this study is based) may include 25–40 functional groups ranging from primary producers to marine mammals, and incorporating a number of fishing fleets for which catches, discards and bio-economical details are provided. An overview of fish species mentioned in this paper, along with elements of their scientific classification, is given in Table 1.

The present study is based on a total of 23 ecosystem models, all of which are available from the first author (see also <http://www.ecopath.org>). The models describe 15 geographical areas, and are each made to represent a given year or short time period between 1880 and 1998 (see Table 2). Many of the models

incorporate time-series information in addition to the year-specific information on which the model description is based (see references in Table 2 for further details). The time-series information is used to assess how well the model can replicate trends over time in the ecosystem as part of what may be considered a validation procedure. This, however, has limited implications for the present study, which does not incorporate the time-dynamic aspects usually considered when using the Ecosim routine of EwE (see Walters *et al.* 1997, 2000).

For nearly all models, the time periods have been chosen to take advantage of available data sources. Notably, the start of biomass data from stock assessment has often dictated the period to be used for the models. The only models that break with this trend are the two historic models for the North Sea

Table 1 List of common names of fish species mentioned in this paper along with corresponding scientific and family names.

Common name	Scientific name	Family
Anglerfish	<i>Lophius piscatorius</i>	<u>Lophiidae</u>
Black seabass	<i>Centropristis striata</i>	<u>Serranidae</u>
Blackspot seabream	<i>Bagellus bogaraveo</i>	Sparidae
Bluefin tuna	<i>Thunnus thynnus</i>	<u>Scombridae</u>
Bluefish	<i>Pomatomus saltatrix</i>	<u>Pomatomidae</u>
Brill	<i>Scophthalmus rhombus</i>	<u>Scophthalmidae</u>
Capelin	<i>Mallotus villosus</i>	<u>Osmeridae</u>
Cod	<i>Gadus morhua</i>	Gadidae
Dogfish	<i>Squalus acanthias</i>	Squalidae
Forkbeard	<i>Phycis phycis</i>	Phycidae
Goosefish	<i>Lophius americanus</i>	<u>Lophiidae</u>
Greenland halibut	<i>Reinhardtius hippoglossoides</i>	Pleuronectidae
Haddock	<i>Melanogrammus aeglefinus</i>	Gadidae
Hake	<i>Merluccius merluccius</i>	Merlucciidae
Halibut	<i>Hippoglossus hippoglossus</i>	Pleuronectidae
Herring	<i>Clupea harengus</i>	Clupeidae
Horse mackerel	<i>Trachurus trachurus</i>	Carangidae
Mackerel	<i>Scomber scombrus</i>	Scombridae
Menhaden	<i>Brevoortia patronus</i>	Clupeidae
Pollock	<i>Pollachius virens</i>	Gadidae
Saithe	<i>Pollachius virens</i>	Gadidae
Salmon	<i>Salmo salar</i>	Salmonidae
Sea trout	<i>Salmo trutta trutta</i>	Salmonidae
Silver hake	<i>Merluccius bilinearis</i>	Merlucciidae
Spiny dogfish	<i>Squalus acanthias</i>	Squalidae
Striped bass	<i>Morone saxatilis</i>	Moronidae
Sturgeon	<i>Acipenser sturio</i>	Acipenseridae
Summer flounder	<i>Paralichthys dentatus</i>	Paralichthyidae
Turbot	<i>Scophthalmus maximus</i>	Scophthalmidae
Weakfish	<i>Cynoscion regalis</i>	Scianidae
Whiting	<i>Merlangius merlangus</i>	Gadidae

(1880s), and for the Newfoundland area (1900). We have included these models to provide extremes on the temporal scale, and fully realize that the biomass estimates used in these models are more uncertain than those in the more current models. Therefore, we also investigate the impact that these and other models have on the overall results, as is described in more detail below.

We have also sought to include models that are extreme with regard to other characteristics; a notable example is the Lancaster Sound model from North-eastern Canada. Reflecting the typical characteristics of such an arctic system, the model includes a variety of marine mammal groups, but only very limited amounts of high-trophic level fishes; in

addition, a large part of the area is ice covered part of the year.

Our initial selection of available models included two that we later chose to exclude from the analysis. One of these described the Icelandic waters in 1950, but did not include any biomasses that were based on empirical data. The other, from the Cantabrian Sea, covered the narrow shelf area only, and our 0.5° by 0.5° spatial cells did not represent this area in a realistic fashion; hence, we would attribute the biomasses to unrepresentative depths.

Because of the uncertainty about abundance of small fish in the North Atlantic in general, we focus on the larger, predatory fishes for which much more information is available, notably through stock assessment and research surveys. We define the predatory fishes as those fish groups for which the trophic level is estimated to be 3.75 or more. This effectively means that we include all fish groups that predominantly eat prey species that feed on fish, zooplankton and/or small benthic organisms (i.e. we excluded all primarily planktivorous, herbivorous and detritivorous fishes).

We also exclude marine mammals and birds as well as high-trophic level invertebrates from our analysis. Marine mammals are better dealt with in a separate study using a different methodology (see Kaschner *et al.* 2001) while for marine birds and invertebrates, it is a consequence of their representation being fairly superficial in the ecosystem models we have at hand. We also note that the biomasses involved for these groups are negligible in any case.

Generalizing slightly, the high-trophic level fishes may be considered to constitute what is commonly called 'table fish'. To illustrate this, a list of fish groups included in the high-trophic level fish category is presented in Table 2. It reflects that the species included are those of main interest for human consumption.

The definition of the trophic level cut-off point chosen here is somewhat arbitrary, and indeed a few groups are included, which we would not normally consider predatory while in a few other cases, some groups one would expect to see included have been excluded. The reason for this may well be that the trophic-level estimation depends on how well the diets (from which the trophic levels were estimated) have been defined, something we have not been able to standardize completely between models. However, the general patterns emerging from the selections are very much in accordance with expectations, e.g. few species (but fairly high biomasses on continental shelves) in the colder, northern areas as compared to

Table 2 Overview of ecosystem models used for estimating abundance patterns of predatory fish in the North Atlantic.

Area	Year	Cells	Fish groups with trophic level > 3.75	Reference
North Sea	1880	369	Bluefin tuna, halibut and turbot, saithe, cod, whiting, sharks, other predatory fish, rays and skates, sturgeon, haddock, horse mackerel, salmon and sea trout, gurnards, mackerel, west mackerel, brill, other prey fish	Mackinson (2001)
Newfoundland (2J3KLNO)	1900	563	Greenland halibut, cod, large pelagic feeders, skates, piscivorous small pelagic feeders	Heymans and Pitcher (2002b)
Faroe Islands	1961, 1997	132	Greenland halibut, cod, saithe, other deep water, other demersal fish	Zeller and Freire (2001), Zeller and Reinert (2001)
North Sea	1963, 1974	369	Saithe, cod, whiting, west mackerel, haddock, other predators, rays, mackerel, gurnards, horse mackerel, herring	Christensen <i>et al.</i> (2002)
Gulf of Biscay	1970, 1998	51	Extra-large pelagics, large sharks, tuna-like fishes, large deepwater fishes, small sharks	Ainsworth <i>et al.</i> (2001)
Lancaster Sound	1980	169	Greenland halibut	Mohammed (2001)
North Sea	1981	369	Saithe, other predatory fishes, whiting, cod	Christensen (1995)
Scotian shelf	1982	160	Demersal piscivores, transient pelagics, halibut, dogfish, cod, silver hake, pollock	Bundy (2002)
Gulf of Maine & Georges Bank	1982	77	Summer flounder, large pelagic feeders, bluefin tuna, bluefish, cod, large demersal feeders, pollock	Heymans (2001)
Morocco	1984	99	Large pelagics, very large demersals, large deepwater fishes, large and medium bathypelagics, small demersals, large demersal. sharks/rays, other sharks/rays	Stanford <i>et al.</i> (2001)
Chesapeake Bay	1985	4	Bluefish, summer flounder, weakfish, striped bass	Baird and Ulanowicz (1989)
Gulf of St. Lawrence (4RS)	1986	58	Greenland halibut, large cod, skates, large pelagics	Morissette 2001)
Newfoundland (2J3KL)	1986	563	Greenland halibut, cod, large pelagic feeders, skates, piscivorous small pelagics	Bundy <i>et al.</i> (2000)
US South Atlantic States	1996	81	Billfishes, sharks, tuna, mackerel, snappers, groupers, jacks, pelagic piscivores, demersal piscivores, benthic piscivores	Okey and Pugliese (2001)
Norwegian-Barents Sea	1997	2307	Cod	Dommasnes <i>et al.</i> (2001)
Newfoundland (2J3KLNO)	1997	563	Greenland halibut, dogfish, pollock, transient pelagics, cod, transient mackerel, large demersal piscivores, skates	Heymans and Pitcher (2002a)
Greenland, west coast	1997	218	Greenland halibut, cod	Pedersen and Zeller (2001)
Iceland	1997	288	Greenland halibut	Mendy and Buchary (2001)

Table 2 continued

Area	Year	Cells	Fish groups with trophic level > 3.75	Reference
Azores	1997	240	Pelagic large predators, large deepwater fishes, large sharks coastal large predators, demersal large predators, <i>Phycis phycis</i> , <i>Pagellus bogaraveo</i> , coastal medium predators, medium sharks, medium demersal invertebratefeeders, rays, medium demersal predators, medium predators	Guénette and Morato (2001)
US Mid Atlantic Bight	1998	48	Billfishes, tunas, bluefish, goosefish, striped bass, weakfish, coastal sharks, spiny dogfish, jacks, benthic piscivores, snapper/groupers, black seabass, demersal piscivores, cods and hakes, redfish	Okey (2001)

Statistical area codes, where appropriate, are given in brackets for clarification. The third column indicates the number of 0.5° spatial cells covered by each model. The lists of fish groups indicate the selection used for estimating abundance. See the individual models for further information about the groups.

the more species-rich warmer, southern areas. We believe the sheer mass of information will outweigh the few cases where the trophic-level estimates were problematic.

Assigning models to strata

The ecosystem model coverage of the North Atlantic is incomplete, precluding simple scaling of flows and rates from the individual ecosystem to the basin level, and calling for a stratification scheme. The scheme we have chosen builds on the structure that is applied for catches and other data in the SAUP databases: 0.5° by 0.5° spatial cells (Watson *et al.* 2001).

Each of the ecosystem models covers a distinct geographical area consisting of a variable number of the 0.5° spatial units (see Fig. 2). As part of the present study, we have constructed a spatial model for each ecosystem using the Ecospace model incorporated in the EwE Software (Walters *et al.* 1999). Ecospace incorporates an Ecosim model in each spatial, non-land cell. In total, the models covered 24% of the area of the North Atlantic, with the coverage reaching 40% in the depth strata where most concentrations of high trophic levels occur (Table 3).

Exchange between spatial cells is modelled for each time step (typically monthly) while accounting for food availability, predation and fishing patterns.

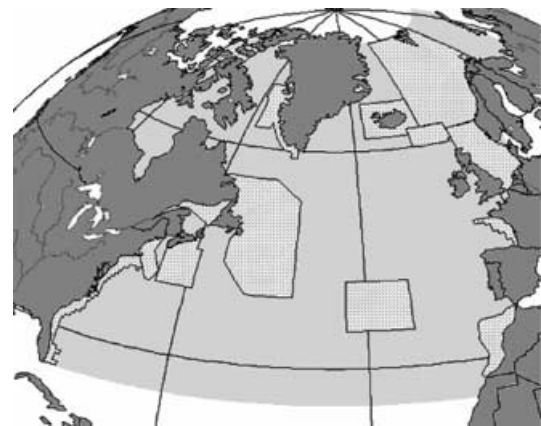


Figure 2 Map of the 15 geographical areas in the North Atlantic for which a total of 23 ecosystem models (shaded polygons, hatched background) were used to obtain estimates for a total of approximately 18 000 0.5° by 0.5° spatial cells (shaded grey background). The total water area included in the analysis is 28 million km². All the models for the Newfoundland/Grand Banks area off Canada do not cover the same area.

Table 3 Area covered by Ecopath models from the North Atlantic, total area and proportion of total area covered by Ecopath models.

Depth stratum (m)	Area covered (1000 km ²)	Total area (1000 km ²)	Proportion
0–10	73	200	0.37
11–50	472	1150	0.41
51–100	576	1408	0.41
101–200	754	2177	0.35
201–1000	1413	3507	0.40
>1000	3567	19683	0.18
Total	6855	28124	0.24

The Ecospace models were constructed based on general information (consulting FishBase) about habitat and depth preferences for the functional groups of the ecosystems. Primary production was distributed spatially based on SeaWiFS data as described below, while fishing effort was distributed spatially based on distance to coast, depth zone preferences of fleets and fish abundance. Fleet definitions varied between models, and the characteristics were based on general knowledge of the fisheries of the North Atlantic.

For each of the spatial model, the cells were distributed between habitats based on depth only. The following depth strata were used for all models: (i) <10 m, (ii) 11–50 m, (iii) 51–100 m, (iv) 101–200 m, (v) 201–1000 m and (vi) >1000 m (Table 3). Depth information at the 0.5° by 0.5° scale was obtained from the ETOPO5 data set available on the US National Geophysical Data Center's Global Relief Data CD (<http://www.ngdc.noaa.gov/products/ngdc.products.html>) as implemented in the 'Sea Around Us' project database (<http://saup.fisheries.ubc.ca>).

The predicted distributions in Ecospace models show marked sensitivity to primary productivity patterns (Martell *et al.* 2002). We therefore cooperated with the Institute for Environment and Sustainability of the European Commission's Joint Research Centre in Ispra, Italy to obtain global primary productivity maps based on SeaWiFS data. The primary productivity maps are based on a model that incorporates the SeaWiFS estimated chlorophyll, photosynthetically active radiation and sea surface temperature patterns (Hoepffner *et al.*, unpublished data) based on the model of Behrenfeld and Falkowski (1997). The maps are available on a monthly and quarterly basis from October 1997 onwards ([\[www.me.sai.jrc.it\]\(http://www.me.sai.jrc.it\)\) but for the present study, a 1-year production average representing 1999 was used, as this was the only yearly average available.](http://</p>
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The primary productivity maps have a spatial resolution of approximately 0.16°, while the database used for the present study operates with 0.5° latitude by 0.5° longitude cells, i.e. with a resolution of one-ninth of the SeaWiFS resolution. Therefore, a facility was included in Ecospace that aggregates the finer resolution maps, averaging while maintaining the overall mean, and prepares the basemap for the Ecospace modelling (for details, see the EWE User's Guide, available at <http://www.ecopath.org>).

Temperatures at 10 m depth were obtained from a climatology based on the NOAA World Ocean Atlas 1998 (<http://www.nodc.noaa.gov/OC5/wod98v2.html>) as implemented in the 'Sea Around Us' Project database. Ice cover information was obtained from the US National Snow and Ice Data Centre, Boulder, Colorado (<http://www.nsidc.org/index.html>), in form of monthly limits of sea-ice coverage.

The environmental parameters are treated as static in this analysis, even though they, in reality, show considerable interannual variability. We do not, however, have access to time series of environmental data at the North Atlantic level and covering the time period of interest (as such data do not exist).

Fisheries catches

There is a relationship, but not a simple one, between the fish biomasses at any given time and how much fish may have been caught. If catches were high, there must have been some high biomasses present to support these catches. However, high biomasses may also be associated with low catches, if the reason is low fishing effort. However, we do not have reliable data on development of fishing effort over time either for the North Atlantic as a whole or for any major parts of the basin; hence, it is not straightforward to deduct overall biomass level from total catches. We expect, however, that the catch composition will change as a function of the biomass level of the preferred fishing target, i.e. of the high-trophic level species. It is by now well established that fisheries expansions go hand in hand with the process of 'fishing down the food web' (Pauly *et al.* 1998), and we can therefore use the catch composition by spatial unit to draw inferences about the overall biomass of high-trophic level fish species (see below).

The catches entering the regression analyses come from the ecosystem models, which in turn have

utilized numerous sources (see model references in Table 2). For this purpose, a routine has been added to the Ecopath software that allows allocation of catches of ecosystem groupings to the catch categories used in the SAUP database, as described further below. In order to carry out this allocation, we extracted catch distributions by the International Standard Statistical Classification for Aquatic Animals and Plants (ISSCAAP) categories (see <http://www.fao.org> for details of this classification) for the years and areas covered by the individual models, and used this to guide the distribution for the groups where the allocation was not obvious.

The catches in the SAUP database are used for predictive purposes based on the biomass regression. Catch data for 1900 were obtained from a variety of published sources and archives (Evermann 1904; Alexander 1905a,b; ICES 1906; Anonymous 1919, 1949, 1978; Cushing 1987; Sahrhage and Lundbeck 1992; López Losa 2000). The main source for the catches from 1950 onwards is the FAO catch database (<http://www.fao.org>), with information added from the Statlant database maintained by the International Council for the Exploration of the Sea (ICES: <http://www.ices.dk>), as well as from ICES assessment working group reports. Spatial distribution of the catches was undertaken using an elaborate, rule-based procedure implemented and described by Watson *et al.* (2001). For this, the statistics were progressively disaggregated based on known distributions for the taxa, hydrographic conditions, and on where reporting countries were permitted access through fisheries agreements in the individual years.

The catches are distributed in 12 categories: (i) anchovies, (ii) herrings, (iii) perches, (iv) tunas and billfishes, (v) cods, (vi) salmoniformes, including smelts and capelin, (vii) flatfishes, (viii) scorpionfishes, including redfish, (ix) sharks and rays, (x) crustaceans, (xi) molluscs and (xii) 'other' groups.

For the regression analysis in the present study, we merged herrings and the salmoniformes (the latter being totally dominated by capelin). There are indications, both from the catches and ecological studies, that capelin replaced herring during the 1970s–1980s when herring abundance in the northern Atlantic was low (Gjøsaeter and Bogstad 1998). Also, the two species serve as important forage species for the high-trophic level species considered in this study. We chose to combine the two invertebrate groups (x) and (xi) in the regression analysis based on the expectation that high invertebrate catches are associated with low biomass levels of

high-trophic level catches (an effect of 'fishing down the food web'), and noting that it did not have any observable effect on the regressions; hence, one variable less is to be preferred.

Finally, when examining the regression, it was clear that the overall catches of tuna and billfishes show very little trend over the 50-year period under study (linear slope 0.1% of intercept, $r^2 = 0.01$, $SD = 12\%$ of mean). This is in accordance with expectations as the catch composition of tuna has changed over the 50-year period; indeed, we now have evidence for declining mean trophic levels of catches within the tunas (Pauly and Palomares 2001). Illustrative of this is that bluefin tuna catches were estimated to be 38 000 tonnes in 1960 and 100 tonnes in 1999, while the decrease was compensated for by increased catches of smaller, lower trophic level tunas so as to maintain (within 1%) the total tuna catch. Thus, the tuna and billfish category turned out not to be a significant predictor of the biomass of high-trophic level fishes, and the category was omitted as a predictive variable from the regression analysis.

Regression analysis

We used multiple linear regression techniques as implemented in S-Plus 6 software for all regression analysis (Anonymous 2001b). Prior to performing the regression analyses, we used an additive and variance stabilizing transformation (AVAS), of S-Plus to study how individual variables are best transformed to obtain linearity (Fig. 3). AVAS seeks for transformations, $\Theta(y) = \phi_1(x_1) + \phi_2(x_2) + \dots + \phi_p(x_p) + \varepsilon$, which provides a good additive model approximation for the data, $y_i, x_{i1}, \dots, x_{ip}$, for $i = 1, 2, \dots, n$, while seeking to achieve variance stabilization. Based on the AVAS analyses, we concluded that logarithmic transformations were suitable for primary production and biomass, while no transformations were required for year and latitude. For depth, indications pointed to the use of a quadratic transformation (truncated at 5000 m to avoid extrapolation). Ice cover was treated as a categorical variable (no ice cover, ice cover part of the year, and ice cover year round) and hence required no transformation. The various catch categories, as defined above, were transformed using logarithmic transformations (catch in $\text{kg km}^{-2} \text{year}^{-1}$, with $1 \text{ kg km}^{-2} \text{year}^{-1}$ added to enable log-transformation of catches of zero).

As data material for the regression analysis, we extracted 7811 records based on the 0.5° by 0.5° spatial cells of the 23 ecosystem models. Each of the

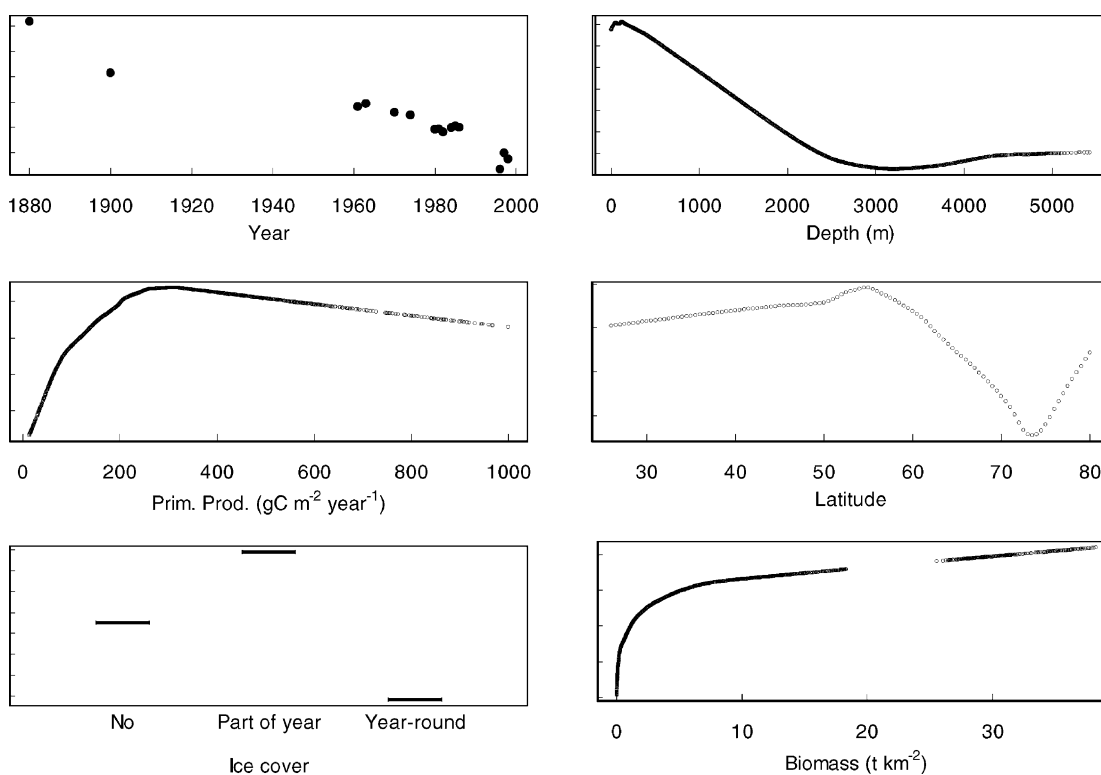


Figure 3 Additive and variance stabilizing (AVAS) transformations indicating how parameters (x-axis) may be transformed (*y*-axis indicate biomass, linear scale) to linearize the individual parameters while considering their joint effects. Results indicate that no transformations are required for year and latitude, while a quadratic transformation is acceptable for depth, and log-transformations for primary production and biomass. Ice cover is treated as a categorical variable.

records included estimates of biomass and catch of high (≥ 3.75)-tropic level fishes, depth, distance from coast, water temperature at 10 m depth, ice cover category, number of seamounts and reefs, primary production, an upwelling index based on latitude and basin-specific temperature anomalies, catch by each of the catch categories defined above, latitude and year of the model.

We were not able to use the following as predictive variables: distance from coast (it appears that the North Atlantic is so accessible that any fishing ground will be exploited; fishing was indeed the reason Europeans started crossing the Atlantic regularly); number of seamounts and reefs (both are negligible) and the upwelling index (there are so few upwelling areas in the study area that no effect can be expected in the regressions). Further, we could not demonstrate any effect of temperature, probably because of the inclusion of the latitude and ice cover terms.

To prevent the records extracted from models covering large areas from swamping those from other models, each of the records were weighted in the

regression analysis using the inverse of the square root of the number of non-land cells as weighting factor in the models to which the given records belong.

The multiple linear regression takes the following form,

$$\begin{aligned} \log(\text{biomass}) = & a + b_1 \cdot \text{year} + b_2 \cdot \log(\text{PP}) \\ & + b_3 \cdot \text{depth} + b_4 \cdot \text{depth}^2 \\ & + b_5 \cdot \text{latitude} + b_6 \cdot \text{ICE}_{\text{part of year}} \\ & + b_7 \cdot \text{ICE}_{\text{year round}} \\ & + b_8 \cdot \log(\text{catch anchovies}) \\ & + b_9 \cdot \log(\text{catch herring and smelts}) \\ & + b_{10} \cdot \log(\text{catch perciformes}) \\ & + b_{11} \cdot \log(\text{catch cods}) \\ & + b_{12} \cdot \log(\text{catch flatfishes}) \\ & + b_{13} \cdot \log(\text{catch scorpionfishes}) \\ & + b_{14} \cdot \log(\text{catch invertebrates}) \end{aligned}$$

where a is the regression intercept, and b_1 to b_{14} the slopes to be estimated by the regression;

biomass is the predicted biomass of predatory fishes (g m^{-2});

PP is the average primary production ($\text{gC m}^{-2} \text{year}^{-1}$);

depth is the average depth (m);

latitude is the latitude of the observation;

ICE_{Part of year} and ICE_{Year round} are categorical parameters that take the value 1 if the cell is ice covered part of the year or year round, respectively, and the value 0 if not and catch variables are in $\text{kg km}^{-2} \text{year}^{-1}$, with $1 \text{ kg km}^{-2} \text{year}^{-1}$ being added to accommodate log-transformations for zero catches.

Based on the 7811 records described above, the regression coefficients and test statistics in Table 4 were obtained (see also Fig. 4). The multiple R^2 of the regression is 0.859 with 7796 degrees of freedom. The F -statistic is 3389 on 14 and 7796 degrees of freedom, with a P -value of 0. (Given spatial autocorrelation, we do not believe our cells to provide true degrees of freedom, yet the results indicate that the regression is fairly robust.) The residual standard error is 0.1280 on 7796 degrees of freedom. All parameters are highly significant ($P < 0.001$).

Summing up the regression results, we conclude that the predictive variables are able to explain the major part of the variance in the data set ($R^2 = 0.86$), and the slopes have the right sign for the variables where we had expectations about their impact. The

t -values give indications for the internal 'ranking' of the parameters, i.e. which ones matter most (or where the probability of exceeding the t -value by chance is smallest). Due to covariation between variables, we acknowledge that any interpretation of the 'rankings' should be treated with extreme caution. The highest t -value is associated with the year parameter, followed by the intercept, latitude and depth. Primary production has a surprisingly low t -value, partly reflecting that depth and primary production show covariance, and partly that we do not have models covering the Gulf Stream region across the North Atlantic where primary production and depth both are fairly high.

As with any other multiple regression, the results are depending on the data material, and we need to consider what we included in the analysis, both with regard to outliers and predictive variables. To study this further, we have conducted a series of analyses, subsampling from the original data sets. This is described in more detail in the following sections.

Effect of individual models on the regression analyses

The regressions we obtain will depend on what observations (here, ecosystem models) we include. To study the robustness of the regressions, we have analysed the data using a jackknife approach (Sokal and Rohlf

Table 4 Parameter estimates and associated test statistics for multiple linear regression to predict the biomass ($\log, \text{g m}^{-2}$) for predatory fishes ($\text{TL} > 3.75$) in the North Atlantic during the second half of the 20th century.

Variable	Value	Standard error	t -value	Pr(> t)	Transformation
Year	-0.017415	0.000255	-68.3	0.000000	None
(Intercept)	35.873360	0.541	66.3	0.000000	None
Latitude	-0.0458485	0.000858	-53.4	0.000000	None
Depth	-0.0009162	0.0000194	-47.2	0.000000	Quadratic
Catch, anchovies	-0.2390645	0.00731	-32.7	0.000000	Logarithmic
Catch, herring and capelin	0.1216986	0.00387	31.5	0.000000	Logarithmic
Catch, scorpionfishes	0.116684	0.00382	30.5	0.000000	Logarithmic
Catch, perches	-0.1420623	0.00472	-30.1	0.000000	Logarithmic
Catch, cods	0.1119097	0.00495	22.6	0.000000	Logarithmic
Depth ²	0.000000089	0.000000005	19.5	0.000000	Quadratic
Catch, flatfish	0.0520826	0.00350	14.9	0.000000	Logarithmic
Ice cover, year-round	-0.2849061	0.0224	-12.7	0.000000	Factor
Catch, invertebrates	-0.0269938	0.00290	-9.3	0.000000	Logarithmic
Primary production	0.1646445	0.0195	8.4	0.000000	Logarithmic
Ice cover, part of year	0.0381208	0.0115	3.3	0.0008919	Factor

The primary production (PP) is in $\log, \text{gC m}^{-2} \text{year}^{-1}$, while catches are in $\log, \text{kg km}^{-2} \text{year}^{-1}$. Depth is included with a linear and a quadratic term. The variables are arranged by t -value (value relative to standard error, given).

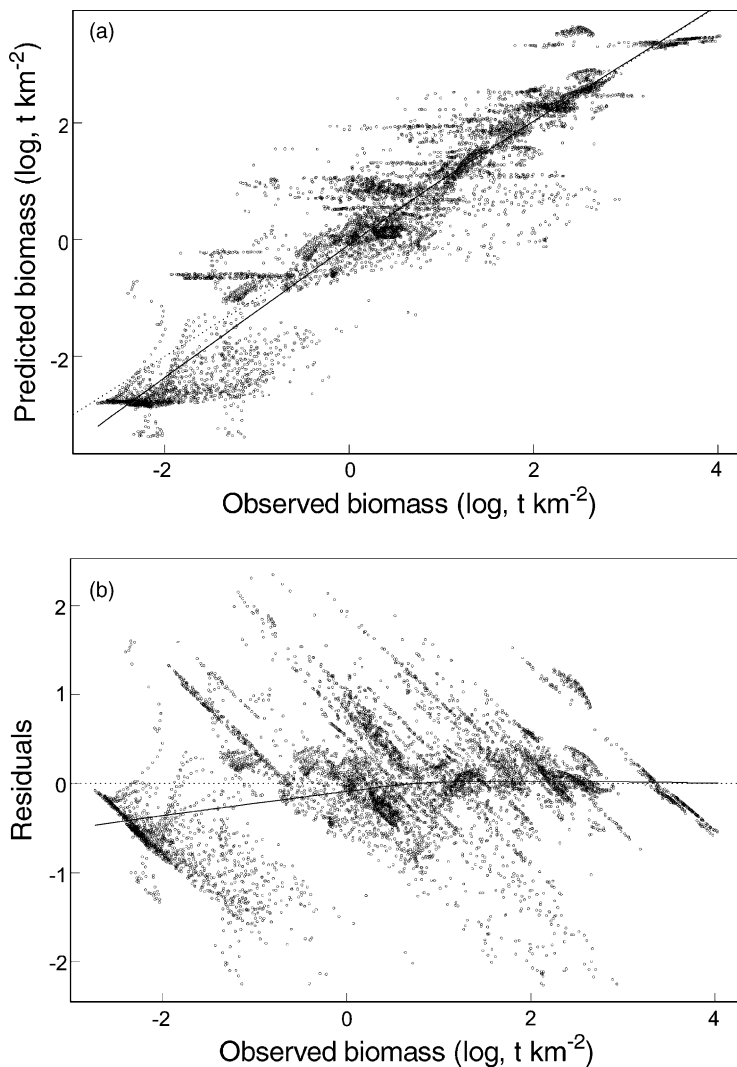


Figure 4 (a) Observed versus predicted biomass (log-scales, tonnes km^{-2}) for predatory fish in the North Atlantic during the 20th century. Solid line indicates average trend. (b) Plot of residuals (predicted–observed biomass, log-scale) versus observed biomass (log-scale, tonnes km^{-2}) for predatory fish in the North Atlantic during the 20th century. Solid line indicates average trend.

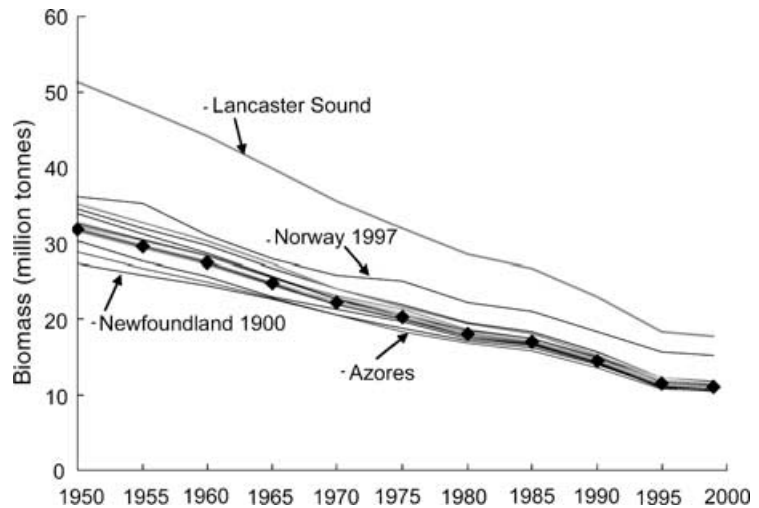
1995), omitting one model at a time from the regression. The details of jackknife analysis are presented by Christensen *et al.* (2001). The jackknife approach can be used in a formal context for estimating confidence intervals of biomasses but because of the small number of observation groupings (models) and the use of a logarithmic scale, the confidence intervals that could be derived here are too wide to be meaningful. We do not find that the standard method for estimating confidence intervals based on jackknifing is applicable to the analyses in the present study, and hence we are for the time being not able to associate confidence intervals with the results.

The biomass trends resulting from the jackknifing are presented in Fig. 5; it is clear that omitting the Lancaster Sound model would lead to nearly twice

as high biomass estimates for the North Atlantic basin, and illustrates the importance of including extremes (here, a temperature extreme with low fish biomasses) in the multiple linear regressions. The model, which if omitted would result in the second highest biomasses, is that for the Norwegian Sea and the Barents Sea, reflecting the same point.

The most noteworthy finding from the jackknife analysis is that while the absolute estimates of abundance are sensitive to inclusion or exclusion of individual models, the overall trends over time show remarkably little sensitivity to model deletion. Hence, the overall conclusions from the present study are not very sensitive to the model selection. Rather, they are emergent properties based on many models.

Figure 5 Illustrates the effect of excluding individual models from the regression analysis in a jackknife fashion (excluding one model at a time and repeating regression analysis and predictions over time). The thick line with diamond markers indicates the regression with all models included. Jackknifed models are indicated only for the few cases generating stronger deviations from the mean trend. The minus sign indicates removal of that model from the analysis.



Effect of catch composition on the regression analyses

In an exercise analogous to the jackknifing for quantifying the effect of excluding individual models from the regression analyses, we have investigated the effect of excluding each of the nine individual catch categories from the regressions. Omitting individual catch categories was found to have negligible impact on the estimated biomasses of high-trophic level fishes in the North Atlantic, and as can be seen from Fig. 6, nearly all the predicted biomasses fall close to the original regression.

The effects omitting catch categories has on the intercepts and slopes of the biomass regressions are presented in detail by Christensen *et al.* (2001). It is concluded that the intercepts and slopes of the

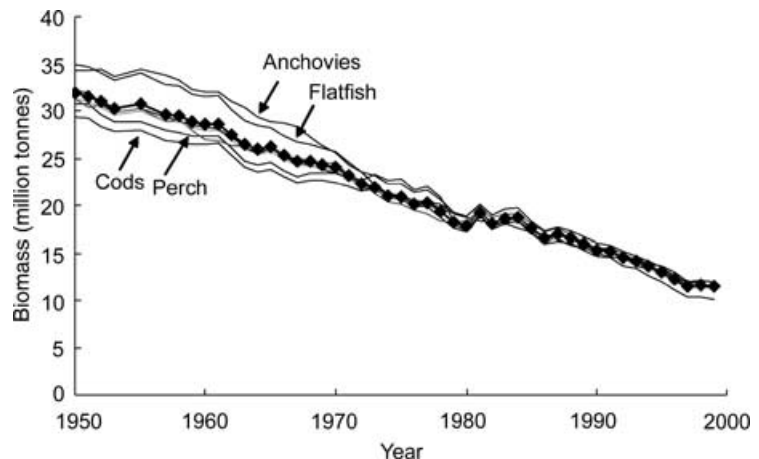
regressions omitting individual catch categories are fairly stable across the analyses.

The overall conclusion from the two series of regression analyses that omitted parts of the data is that the results are robust with regards to the slope of the resulting biomass trends, whereas the absolute values of the predicted biomasses are more uncertain. This is in line with the general expectation for this form of multiple regression, i.e. we expect to be able to distinguish change better than we can predict absolute values.

Predicting biomass of predatory fishes

We have derived a linear regression to predict the abundance of high-trophic level fishes in the North Atlantic based on information from a number of

Figure 6 Effect on the estimated biomass of high-trophic level fish in the North Atlantic of omitting individual catch groupings from the regression analysis. The thicker line with diamond markers is based on the original regression including all catch categories. Groups that when omitted have a noticeable impact on the results are indicated.



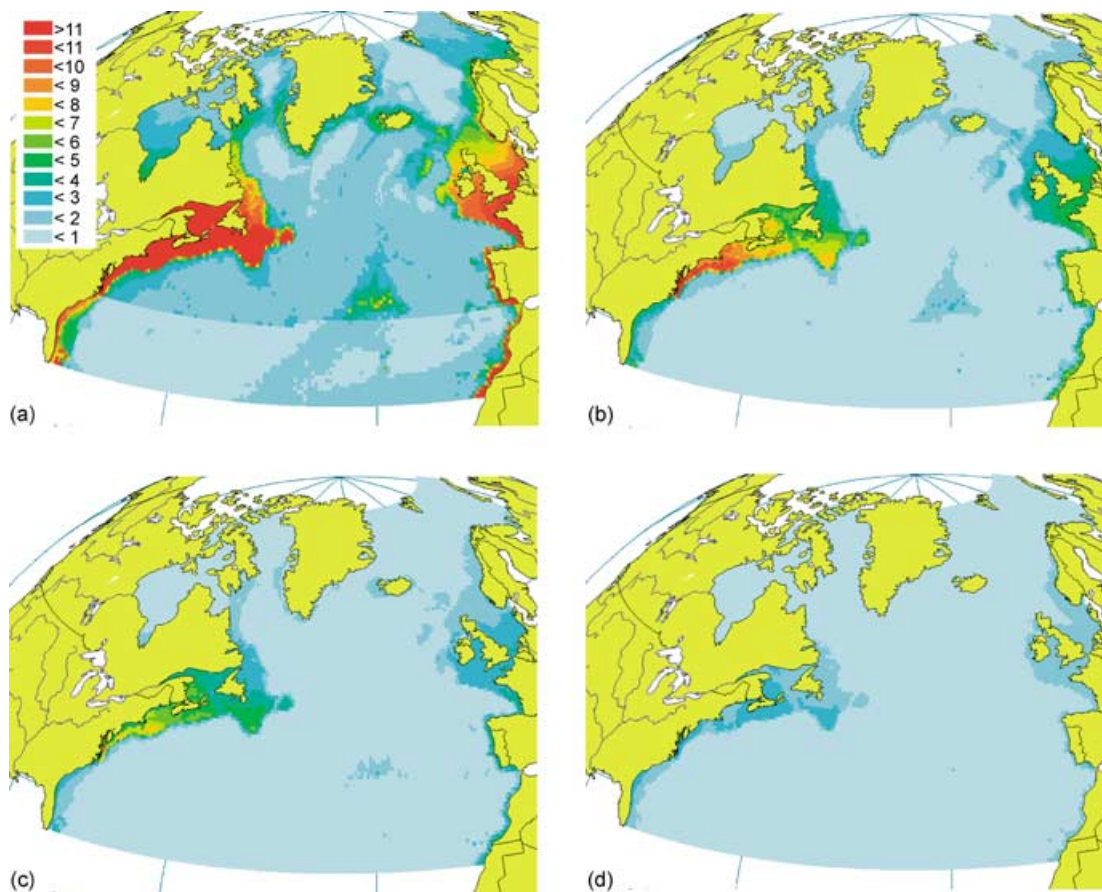


Figure 7 Biomass distributions for high-trophic level fishes in the North Atlantic in (a) 1900 (b) 1950 (c) 1975 and (d) 1999. The distributions are predicted from linear regressions based on primary production, depth, temperature, year, ice cover, latitude and catch composition. Units for the legend are tonnes km^{-2} .

ecosystem models dispersed over the region and in time from the late 19th century through to the end of the 20th century. The regression is based on a total of 18 024 spatial units of 0.5° by 0.5° , and uses year, depth, primary production, temperature, ice cover, and catch quantity and composition to predict the biomass.

For predictive purposes, we then established a spatialized database including the same information for all spatial units globally for 1900, as well as for all years from 1950 through 1999. For the present analysis, however, we use the database only to predict biomasses in the North Atlantic region to avoid extrapolation beyond the area covered by the ecosystem models in Table 2.

Based on the biomass regression analysis applied to the North Atlantic in 1900, 1950, 1975 and 1999, the maps in Fig. 7 were derived. They indicate how biomasses were predicted to be distributed, and are

intended to describe general patterns only as they will obviously miss out on specific events, such as the emergence of a big year-class of a major population for reasons we cannot predict. The maps indicate a strong decline in biomass over the century studied; we will return to this theme below.

Catches

The catches of high-trophic level species, i.e. of the main species of interest for human consumption, increased steadily through to the end of the 1960s, and have declined as steadily since then (Fig. 8). The catch level in the late 1990s was thus lower than that in 1950 in spite of major developments in catch capacity and technological progress, along with geographical expansion across the North Atlantic region.

The estimated spatial distributions of the high-trophic level catches are mapped in Fig. 9. They are

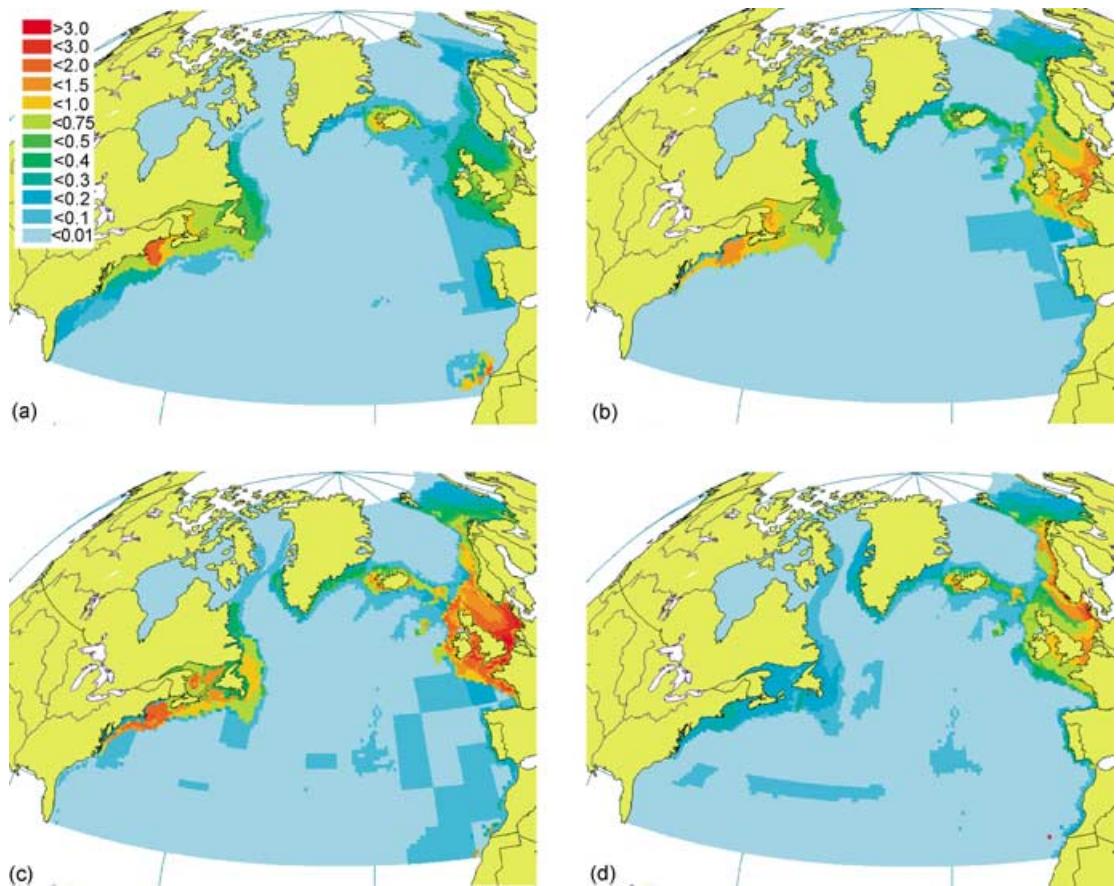
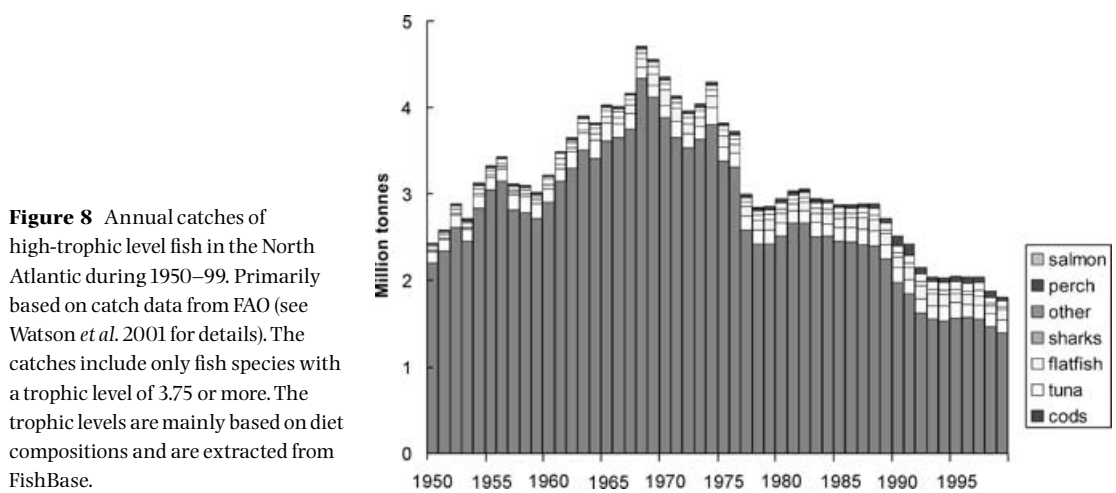


Figure 9 Predicted catch distributions of high-trophic level fishes in the North Atlantic in (a) 1900 (b) 1950 (c) 1975 and (d) 1999. The catches are based on FAO catch data information supplemented with other sources using a rule-based system for spatial allocation (Watson *et al.* 2001), and are here extracted for fish with trophic level ≥ 3.75 (based on trophic levels in FishBase). Units for the legend are tonnes $\text{km}^{-2} \text{year}^{-1}$.

based on the rule-based method for distribution of catches described by Watson *et al.* (2001), but applied only to fish species with a trophic level of 3.75 or more.

Fishing mortalities

The catch figure and catch maps (Figs 8 and 9) by themselves paint a dire picture of what has happened in the North Atlantic area over the last 50–100 years, but they do not directly address a major question: 'Do we catch less because there are less fish, or is it due to catch restrictions imposed to limit catches?' In order to address this question, we need to derive measures of how fishing effort has developed over time. Ideally, we would have a direct measure of the fishing effort, but such information is pathologically poor even in this well-studied and highly regulated region.

In lieu of a direct measure, we will revert to a classic estimation. Beverton and Holt (1957) describe the ratio of catch to biomass for a population as a direct measure of fishing intensity as a surrogate for what is commonly described as 'fishing mortality', the method of choice in fisheries assessment for regulating fishing effort. We emphasize that the measure of fishing mortality we have derived here is not directly comparable to the mortality rates commonly reported as the absolute level of the biomasses estimated here is associated with considerable uncertainty. Therefore, we prefer to interpret the measure as a relative index of 'fishing intensity' only, especially since Beverton and Holt proposed this term for use in spatial applications.

Combining information about catch and biomass levels over time, we obtain the results shown in the maps in Fig. 10 and in the plot in Fig. 11. The figure

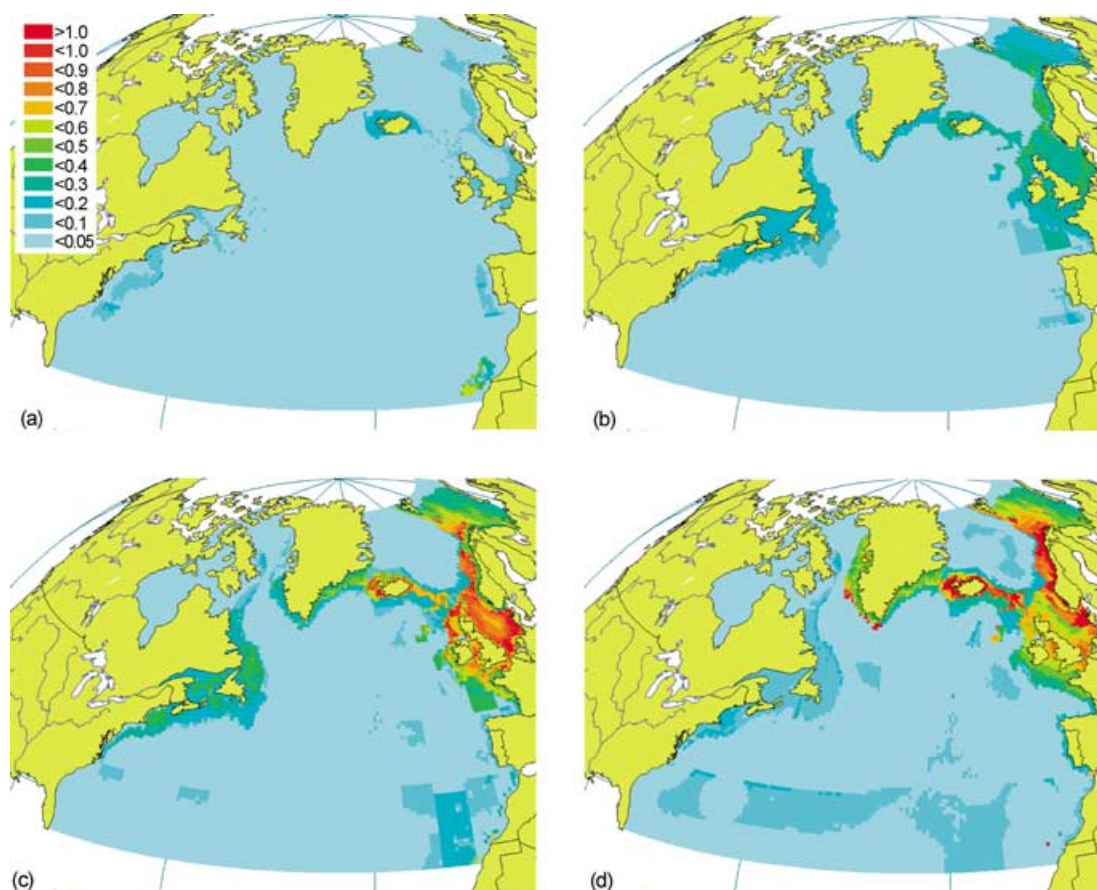
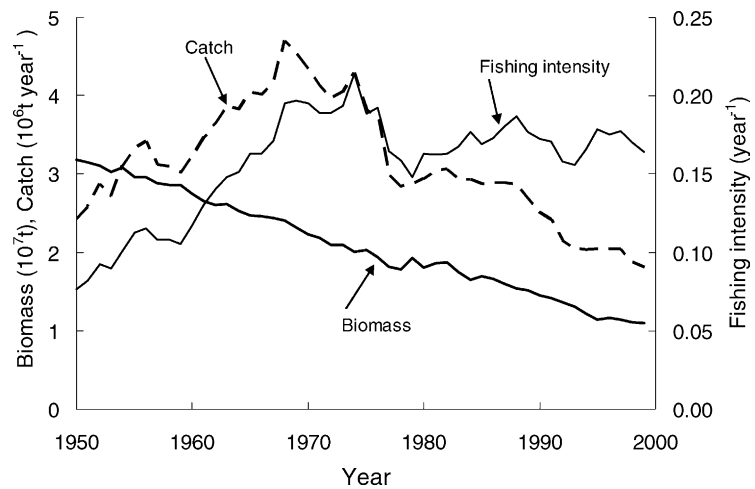


Figure 10 Estimated fishing intensity for high-trophic level fishes (TL \geq 3.75) in the North Atlantic region in (a) 1900 (b) 1950 (c) 1975 and (d) 1999. The fishing effort is derived from spatial estimates of biomasses (Fig. 7) and catches (Fig. 9). Units for the legend are year⁻¹.

Figure 11 Estimated catch (dark broken line, 10^6 tonnes year⁻¹) and biomass (dark solid line, 10^7 tonnes) of high-trophic level fishes in the North Atlantic during 1950–99. The ratio between catch and biomass is an expression of annual fishing intensity (light solid line).



summarizes trends over the last 50 years for high-trophic level fishes in the North Atlantic. Biomasses are found to have been declining steadily over the period at a rate that was slightly lower in the first 20 years than in the last 30 years. The catches peaked in the late 1960s, and have declined steadily since to the extent that the level in 1999 was lower than that in 1950. The resulting measure of fishing intensity, estimated as the ratio between catch and biomass, provides part of the explanation. Fishing intensity increased with catches and has remained nearly constant since the late 1960s, while both catches and biomasses declined steadily.

How long can this continue? There are no indications in the results of a slowing down in the trend of declining biomass. The results thus predict that high-trophic level fishes will be all but gone from the North Atlantic region within a few decades if the current trend continues.

Discussion

Overall, we estimate that the biomass of high-trophic level fish species in the North Atlantic declined by two-thirds during the second half of the 20th century, and by a factor of around nine for the century as a whole. We should ask then, how reliable is this estimate? We note that the finding seems to be fairly robust to the extent that it did not matter much if we omitted part of the data material on which the estimate is built, but despite the jackknifing that led to Fig. 5, we are at present unable to assign a formal confidence interval to the estimate. It is also a fairly difficult task to find supportive evidence in

the form of bottom-up approaches summing up the biomasses of all major fish populations in the North Atlantic. This is reflective of the varying time periods for which assessments have been made for the many populations in the area. Thus, some form for modelling is needed to fill in the blanks, i.e. to provide estimates for the years where none have been made. Also, far from all stocks are being assessed, making a bottom-up estimate likely to be an underestimate.

While waiting for a bottom-up approach, we can examine some trends from various stock assessments in the North Atlantic (Fig. 12). Assembling the plots in the figure was done by reviewing the majority of the recent stock assessments made for the North Atlantic, and extracting biomass time series for high-trophic level fishes. The most difficult task in doing this was to decide which populations to include here – there were so many that virtually all showed the same patterns, be it target or nontarget species: massive decline during the period for which assessments were made, and a presently critical state of the stocks (see Table 5 for an overview of the state of affairs for the majority of the high-trophic level species under ICES auspices). In contrast, there were very few populations that did not show a clear decline over time (such as cod at the Faroe Islands, see Fig. 12).

The pattern that seems to emerge when examining biomass trends for a variety of North Atlantic fish populations is one of massive decline, indicating that the decline over time we are estimating in this study is at least a feasible scenario. This is also the conclusion reached when examining the trends for the high-trophic level species included in the stock

recruitment database assembled by R. Myers (available at <http://fish.dal.ca/~myers/welcome.html>); see Christensen *et al.* (2001) for further details.

Our study indicates that fishing intensity in the North Atlantic increased through the 1950s and

1960s, and has remained at what appears to be an unsustainably high level ever since. For comparison, the trend for fishing mortality in 35 populations in the North Atlantic based on stock assessments is compared to the fishing intensity from our study

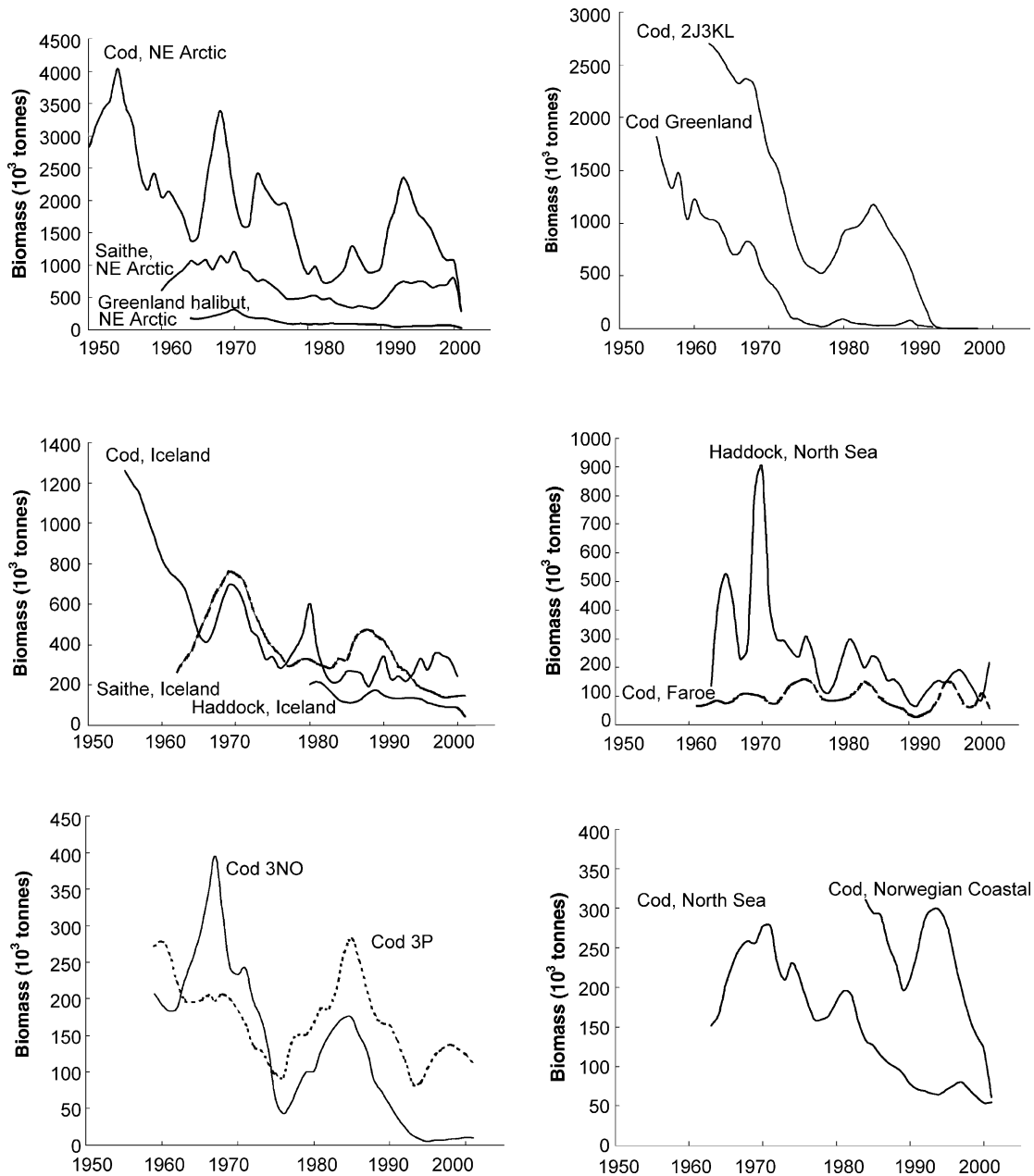


Figure 12 Trend over time (1950–2001) in biomass (thousand tonnes) of a variety of high-trophic level fish stocks in the North Atlantic. The figures are arranged by area with statistical area codes used where appropriate (based on Lilly *et al.* 1998; Bratley *et al.* 2000; NAFO 2000; ACFM 2001; Anonymous 2001a; ICCAT 2001; Lilly *et al.* 2001; O'Brien and Munroe 2001).

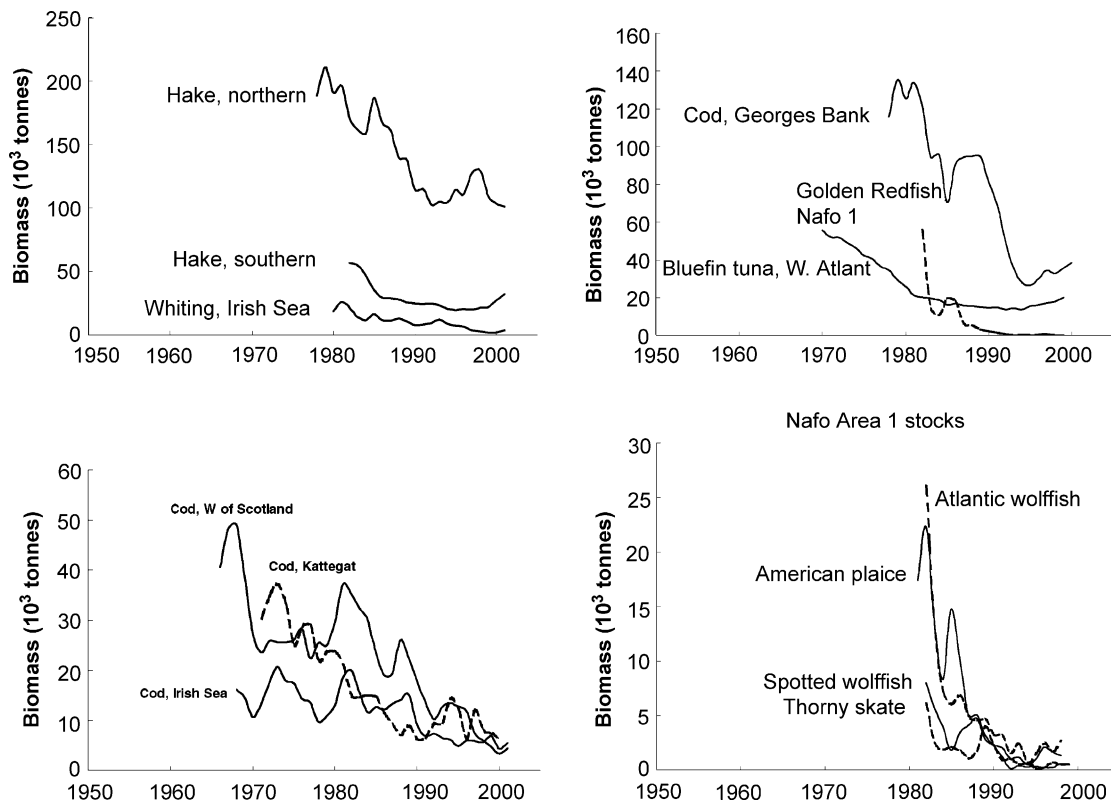


Figure 12 continued

(Fig. 11) in Fig. 13. We conclude from the graph that the two sets of fishing intensity bear much similarity.

Several observations require mentioning when examining Fig. 13; one is the different scaling of the two *y*-axes. Fishing intensity is calculated as the annual catch over the biomass and while our study indicates a ratio approaching 0.20 years^{-1} , the indications of fishing mortalities from the assessments are three times higher. This indicates that the biomasses we estimate are considerably higher than those originating from averaging over the assessed stocks. This apparent difference may have several causes of which two need to be mentioned. First, only some populations are subjected to stock assessment, and these tend to be the ones with highest exploitation rates. Second, biomass estimates based on regressions with log-transformations are quite uncertain, and indeed we trust the trend in biomass more than the face value of the estimates. At present, which of the two explanations provide most toward an explanation is open, but we do expect both factors to be contributing.

We are aware that the mean fishing intensity of assessed stocks presented in Fig. 13 should not be interpreted as the mean fishing intensity for high-trophic level fishes in the North Atlantic. For this, the fishing intensities should have been weighted according to population sizes. However, our intention is rather to discover something about the average population – since the measure of fishing intensity is calculated as catch over biomass, it is a measure of exploitation rate, a probability of being caught and as such an ecologically more representative measure.

The maps and figures presented here indicate that fishing intensity and catch levels have been higher in the North-eastern Atlantic than in the North-western Atlantic. Yet, the decline in biomass of high-trophic level fishes has been most severe in the north-western part of the basin. This may seem inconsistent, but may well result because of the waters of the north-west being colder, deeper and less productive than in the north-east, i.e. the New World waters are less resilient to fishing pressure than those in the Old World. Maps of hydrographic

Table 5 Status of high-trophic level fish stocks in the North-eastern Atlantic according to the ICES Advisory Committee for Fisheries Management (ACFM 2001).

Species	Area	State of stock/exploitation
Anglerfish	North Sea (IV, VI)	Stock is harvest outside of SBL
Cod	NE Arctic (I, II)	Stock is outside of SBL
Cod	Norwegian coastal	Spawning stock is at a historical low
Cod	Greenland (XIV, NAFO 1)	Stock is outside SBL
Cod	Faroe Plateau (Vb1)	Stock harvested outside SBL
Cod	West of Scotland (VIa)	Stock remains outside SBL
Cod	North Sea (IV, VIId, IIIa)	Stock outside SBL
Cod	Kattegat (IIIa)	Stock considered outside SBL
Cod	Kattegat (IIIa)	Stock considered outside SBL
Cod	Irish Sea (VIIa)	Stock remains outside of SBL
Cod	VIIe-k	Stock outside of SBL
Cod	Icelandic waters (Va)	Stock near historic low
Greenland halibut	NE Arctic (I, II)	Stock considered outside SBL
Greenland halibut	Greenland (V, XIV)	Stock harvested outside SBL
Haddock	Faroe (Vb)	Stock outside SBL
Haddock	West of Scotland (VIa)	Stock harvested outside SBL
Haddock	Rockall (VIa)	Stock remains outside SBL
Haddock	North Sea (IV, IIIa)	Stock being harvested outside SBL
Haddock	Irish Sea (VIIa)	Stock harvested outside of SBL
Hake	Southern (VIIx, IXa)	Stock outside SBL
Hake	Northern (IIIa, IV, VI, VIII, VIIIa,b,d)	Stock is outside SBL
Redfish	NE Arctic (I, II)	Stock considered outside SBL
Saithe	NE Arctic (I, II)	Stock within SBL following good year classes
Saithe	Icelandic waters (Va)	Stock considered outside SBL
Saithe	Faroe (Vb)	Stock harvested outside SBL
Saithe	North Sea (IV, IIIa, VI)	Stock is within SBL
Whiting	Irish Sea (VIIa)	Stock remains outside of SBL

ICES statistical area codes are given in brackets. Only two smaller stocks (of saithe) are considered within safe biological limits (SBL).

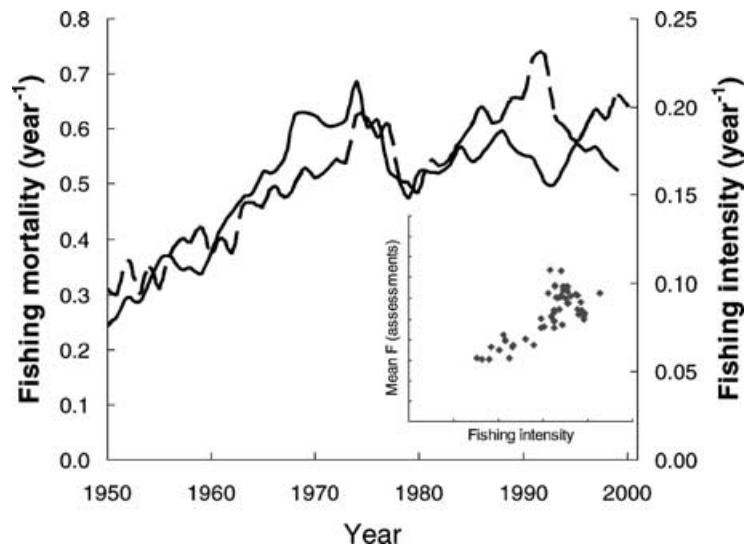
and productivity patterns lend some credibility to such a hypothesis. If this observation has any merit, it means that care should be exercised when transferring experience on managing North-eastern Atlantic stocks to the North-western Atlantic.

In the present study, we were not able to reliably estimate the abundance of forage fishes, and chose to omit these from the results. This is reflective of our limited knowledge of these groups and is indicative of fisheries science focusing on the exploited target species, and largely ignoring the ecology of the systems on which the fisheries rely.

Ecosystem models may indeed help one to draw inferences about prey abundance from predator demand. We can conclude that if the biomasses of predatory fishes were indeed much higher in past ecosystems (as all evidence points to), they must have been consuming more than today's impoverished fauna would lead one to think. However, we do not

know if this demand was met by a higher biomass of the forage species and/or by higher mortality rates for the groups. On the other hand, we can be certain that the product of these two, i.e. the production of prey species must have been higher. We note in passing that there are ways of obtaining supporting evidence – egg and larval surveys have been conducted for a century, and even if they were rather sporadic in the early part of the 20th century, there is a widespread coverage of standardized egg surveys from the 1960s through to the 1980s or beyond. Unfortunately, the surveys have typically focused on target species only, and the eggs or larvae of the species of lower trophic level may not have been analysed. Since the samples are stored in many laboratories, it is, at least in principle, still possible to obtain such information given sufficient interest and resources. Another source of evidence may come from the size compositions of forage species from 'old' diet composi-

Figure 13 Trend in mean annual fishing mortality for assessments of 35 populations of high-trophic level fish species from the North Atlantic (broken line, primary y -axis). Sources are the same as for the biomasses in Fig. 12. The solid line (secondary y -axis) indicates the annual fishing intensity from the present study (Fig. 11). The insert shows the two series plotted versus each other, with the values from this study on the x -axis.



tion studies of predatory fishes. Based on the size distributions, mortality rates can be estimated given readily available growth parameters.

It should be noted that the overall findings of this study are not caused by catch trends over time or for that matter by a systematic error in catch trends over time. Even if the catches are totally omitted from the regression analysis, we obtain a highly significant regression in which the year-term explains most of the change in biomass. Hence, the regression we present in this study does not serve to explain what is causing the changes in biomass, be it environment, fishing pressure or a combination. We do find, however, that the decrease in biomass is associated with a marked increase in fishing pressure. While we fully recognize that environmental changes may impact ocean productivity patterns (see Beaugrand *et al.* 2002), we have no reason to believe that the environmental trend over time would lead to a consistent decrease in the biomass of high-trophic level fishes.

We have developed and applied a methodology to assess the state of the high-trophic level fish populations of the North Atlantic, and have concluded that the biomass of these commercially and ecologically important species is dwindling rapidly. We stress that what happens to the high-trophic level species serves as an indicator for what we do to the ocean, and hence we conclude that all is not well with the ocean.

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